# ON THE ROLE OF THE LOFT, THE DISTANCE AND SITE OF RELEASE IN PIGEON HOMING (THE "CROSS-LOFT EXPERIMENT")

KLAUS SCHMIDT-KOENIG

*Dept. of Zoology, Duke University, Durham, N. C., and Max-Planck-Institut f. Verhaltensphysiologie, Abt. Mittelstaedt, Wilhelmshaven and Seewiesen, Germany*

## The Problem

The idea of "map and compass" as an explanation for the homing orientation of pigeons was originally proposed by Kramer (1953a). The displaced pigeon, it was suggested, first determined its geographical position and then selected the home direction. This concept was inspired by Kramer's (1950, 1951, 1952) discovery of the sun compass in birds, a mechanism suitable for the selection and maintenance of directions. The actual operation of such a mechanism in the process of initial orientation of homing pigeons has subsequently been demonstrated (Schmidt-Koenig, 1958, 1960, 1961). The isolation of the sun compass as one constituent of the homing process supported Kramer's concept. But, although the idea of map and compass had been formulated years ago and though the discussion usually referred to this "map" as a literal representation of the geographical position of displacement, attempts to analyze its necessary components have not been made until recently (Schmidt-Koenig, 1960, 1961). It should be briefly reiterated that "map" means that the position of a displaced bird would have to be established by geographical or other coordinates. It would then be related to home in another step. Two divergent quantities would be involved: the direction and the distance from home. The directional part has been the subject of extensive considerations. However, after Kramer himself (1953b) had briefly touched on the role of distance, no evidence has become known dealing with the precise role of this parameter in the process of homing orientation. Matthews (1955) discussed distance in the light of his hypothesis, contributing some diagrams of poor initial orientation at less than 50 miles and of good initial orientation at more than 50 miles. Good initial orientation at less than 50 miles was also observed, however, and attributed to recognition of landmarks.

The distance from home can be thought of in the following way:

1. It may be directly taken into account by the bird's navigational system.
2. It may merely affect the accuracy of the bird's navigational system.
3. It may be irrelevant to the bird's navigational system. Mechanisms operating exclusively on directional information can be visualized as being relatively simple.

The present attempt to investigate the role of the distance is based on the following consideration: If a number of lofts are established in the shape of a symmetrical cross, with several kilometers' distance between lofts, the inhabitants of these lofts may be released from points along the extension of the axes of this cross. From points close to the cross, birds from certain lofts would face identical home directions but different distances, whereas birds from other lofts would face different directions but similar distances. Going farther away from the cross, these differences would diminish. It was the objective of the study reported here to investigate the effect of such a controlled diversity of parameters on homing within a range of less than 100 km.

This work was supported by grants from the National Science Foundation (nos. G-9816 and G-19849 to P. H. Klopfer and K. Schmidt-Koenig) and by contracts from the Office of Naval Research (Nos. 301-244 and 301-618 with Duke University). I am grateful to Peter H. Klopfer for his continual helpfulness and stimulating discussions, to him and J. P. Hailman for reading and improving the manuscript. I am especially indebted to J. G. Pratt; also to the late C. R. Baucom and his wife, to D. Carr, Durham, and to C. W. Davis and C. Y. Tilson, Chapel Hill, for their kind permission to establish lofts on their estates and for their assistance.

## Experimental Design

In 1960, the Duke University colony was represented by two long-existing lofts, the Baucom loft and the Duke Forest lofts (Kramer, Pratt and St. Paul, 1958). Three more lofts were established in spring, 1960, to form a reasonably symmetrical cross (Fig. 1). The lofts were named according to their location within the cross as "center loft" (Baucom), "east loft" (Duke Forest) and so on.

Two release sites were selected along each of the axes of the cross. The first, short-distance site was located as close as possible to the cross, the second site at about three times the distance between the center loft and the first release site. The exact figures for bearings and distances may be taken from Table I.

## Experimental Procedure

The three new lofts were stocked with youngsters from the Duke Forest and Baucom lofts which were, in turn, inhabited by birds from the "Duke University strain," originally founded (by J. G. Pratt) and eventually supplemented with birds obtained from local pigeon racers (*cf.* Schmidt-Koenig, 1963).

All naive birds were subjected to 3–4 exercise releases from various directions and 5–15 km. from home before they were used for critical cross-loft releases. Orientational pre-experience was kept about equal for all flocks, if necessary by supplementary exercise releases. All releases from the short-distance sites were performed between September and December, 1960, all releases from the longer-distance sites between February and May, 1961. The sequence of releases was designed to avoid successive releases from the same direction.

For releases, the birds were collected at night and driven to the release site the next morning inside a covered pick-up truck. At the release site, the birds were taken singly from covered crates and released with random alternations between birds from the various lofts. Each bird was followed with field glasses to

TABLE I

*Detailed information on bearings and distances from the nine release sites to the various lofts; numerical account of the vector diagrams in Figure 1; homing success for all release sites and lofts. Underlining indicates data pooled from two (exceptionally three) releases. Brackets indicate distributions random at $p > 0.05$*

| Release site name (direction) | Loft | Home | | Vanishing data Direction and length of mean vectors and sample size (as in Fig. 1) | | | | | | Homing success Total of birds | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | distance km. | direction | α | a | n | α | a | n | released | lost |
| Caldwell School (N) | N | 7.0 | 195° | 185° | .56 | 29 | | | | 51 | 4 |
| | E | 22.5 | 174° | 147° | .50 | 30 | | | | 43 | 6 |
| | S | 29.5 | 190° | 158° | .70 | 34 | | | | 37 | 4 |
| | W | 20.0 | 210° | 313° | .61 | 39 | | | | 43 | 3 |
| | C | 21.0 | 192° | 301° | .83 | 26 | | | | 39 | 2 |
| Durham (E) | N | 21.2 | 331° | 268° | .61 | 27 | 144° | .52 | 14 | 34 | 6 |
| | E | 7.6 | 295° | 247° | .69 | 28 | | | | 31 | 7 |
| | S | 16.5 | 261° | 232° | .50 | 30 | | | | 34 | 2 |
| | W | 21.0 | 294° | 238° | .63 | 34 | | | | 49 | 2 |
| | C | 14.5 | 291° | 249° | .81 | 34 | | | | 34 | 4 |
| Chapel Hill (S) | N | 28.0 | 16° | 309° | .55 | 27 | | | | 36 | 4 |
| | E | 15.9 | 41° | 52° | .76 | 22 | (87°) | .19 | 25 | 63 | 4 |
| | S | 5.4 | 19° | (241°) | .17 | 27 | | | | 36 | 1 |
| | W | 16.5 | 356° | 277° | .69 | 27 | | | | 28 | 4 |
| | C | 14.0 | 19° | 269° | .72 | 32 | 191° | .62 | 17 | 52 | 8 |
| Hillsboro (W) | N | 17.0 | 61° | 44° | .64 | 14 | (57°) | .31 | 13 | 36 | 3 |
| | E | 19.6 | 113° | 123° | .65 | 28 | 284° | .55 | 12 | 60 | 11 |
| | S | 16.3 | 149° | 165° | .75 | 28 | 210° | .83 | 13 | 49 | 2 |
| | W | 6.5 | 112° | 111° | .91 | 38* | | | | 49 | 2 |
| | C | 13.0 | 118° | 242° | .66 | 33 | | | | 38 | 2 |
| South Boston (N) | N | 61.3 | 199° | (291°) | .08 | 31 | 194° | .71 | 10 | 54 | 11 |
| | E | 75.5 | 192° | 218° | .68 | 33 | | | | 38 | 4 |
| | S | 83.5 | 197° | 187° | .75 | 34* | | | | 43 | 8 |
| | W | 73.8 | 202° | (297°) | .19 | 38* | 274° | .58 | 11 | 59 | 5 |
| | C | 75.0 | 197° | 221° | .57 | 35 | | | | 39 | 8 |
| Raleigh (E) | N | 51.3 | 310° | 339° | .66 | 33 | | | | 35 | 7 |
| | E | 38.8 | 295° | 298° | .56 | 17 | (258°) | .41 | 14 | 37 | 5 |
| | S | 45.5 | 283° | 281° | .50 | 27 | (139°) | .12 | 15 | 45 | 6 |
| | W | 68.7 | 294° | 294° | .70 | 28 | 1° | .74 | 13 | 45 | 6 |
| | C | 45.5 | 293° | 301° | .72 | 32 | | | | 37 | 3 |
| Sanford (S) | N | 67.8 | 17° | 318° | .69 | 31 | | | | 37 | 0 |
| | E | 54.9 | 27° | 327° | .60 | 26 | 266° | .43 | 16 | 55 | 3 |
| | S | 45.5 | 18° | 322° | .55 | 27 | | | | 36 | 1 |
| | W | 55.5 | 13° | 331° | .81 | 29 | | | | 34 | 2 |
| | C | 54.0 | 19° | 325° | .60 | 36 | | | | 37 | 2 |

* Three releases.

TABLE I—(*Continued*)

| Release site name (direction) | Loft | Home | | Vanishing data Direction and length of mean vectors and sample size (as in Fig. 1) | | | | | | Homing success Total of birds | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | distance km. | direction | α | a | n | α | a | n | released | lost |
| Burlington | N | 40.0 | 96° | *(348°)* | *.11* | *27* | | | | 30 | 5 |
| (W) | E | 47.8 | 115° | *(145°)* | *.13* | *29* | 205° | .60 | 21 | 54 | 8 |
| | S | 43.0 | 122° | *152°* | *.45* | *29* | *201°* | *.69* | *23* | 57 | 5 |
| | W | 34.5 | 117° | *320°* | *.64* | *31* | | | | 32 | 4 |
| | C | 41.0 | 117° | *190°* | *.64* | *32* | 283° | .75 | 16 | 75 | 6 |
| | | | | (309°) | .12 | 13 | | | | | |
| Reidsville | N | 73.0 | 105° | *(123°)* | *.30* | *23* | | | | 25 | 1 |
| | E | 81.5 | 115° | 91° | .86 | 19 | 159° | .59 | 11 | 50 | 11 |
| | | | | (23°) | .27 | 12 | | | | | |
| (W) | S | 76.5 | 123° | *136°* | *.73* | *24* | (—) | .00 | 9 | 40 | 5 |
| | W | 68.4 | 116° | *146°* | *.61* | *29* | (167°) | .31 | 16 | 47 | 1 |
| | C | 75.0 | 116° | *129°* | *.46* | *27* | | | | 33 | 7 |

the vanishing point. The bearings at vanishing were recorded to the nearest 5° interval. The time elapsing between take-off and vanishing was recorded with a stop watch. Recording of homing performance, providing individual homing speeds, would have required five permanent welcomers for each releasing day, an expense beyond our budget. Instead, homing success, as established by the number of birds that did home, was recorded.

## STATISTICAL DESIGN

As a standard procedure, two releases were performed from each site, each involving 15 to 20 (exceptionally more) birds from each loft. This meant the liberation of 75–100 birds within 5–8 hours. The vanishing bearings of the birds from each loft in each release were calculated to give $\alpha$, the direction of the mean vector and a, its length (Gumbel, Greenwood and Durand, 1953). These quantities were then examined for randomness according to Durand and Greenwood (1958) and Greenwood and Durand (1955) and a graph derived from these authors (Schmidt-Koenig, 1961, appendix). The term, "release," subsequently applies to the data from birds of one loft obtained during one releasing day.

The following statistical procedure was adopted for experimenting and also maintained for graphical demonstration (Fig. 1; Table I). If the mean vectors of two releases (*i.e.*, at a given release site from birds of particular lofts) agreed by (a) either being both non-random ($p \leq 0.05$) and different from each other by not more than 35° [1], or if (b) both were random ($p > 0.05$), then the scores of the two releases were pooled and are given in Figure 1 with a double symbol (this applied, for example, to all releases from Caldwell School). If the two vectors

[1] At the time of the experiments, no specific test to discriminate between two circular samples was yet available; 35° was estimated to be reasonable.

either (c) were non-random (levels as above) but differed by more than 35°, or (d) were at random one time and non-random the other time, a third release was performed. Then, the scores of those two releases that met the requirements (a) and (b) were pooled and were plotted in Figure 1 with a double symbol, the other release given in a single symbol (*e.g.*, east loft and south loft at Hillsboro, north loft at South Boston). If all three disagreed, three single symbols were given (*e.g.*, east loft at Reidsville). It was further intended to end with about 30 vanishing scores for what may be termed the "preferred direction." However, a certain proportion of birds usually fails to yield vanishing scores either because the observer loses a few birds from sight before they reach the vanishing point or because some birds join stray pigeons or because some perch. In addition, the population of particular lofts sometimes was too low to afford 15–20 birds for a release. Thus, exceptionally four releases had to be performed, as may be seen from Figure 1 and Table I (*e.g.*, south loft and central loft at Burlington). Detailed information on vanishing data and on homing success may be taken from Table I.

The statistical analysis is, unfortunately, handicapped by the lack of certain methods specific for circular data. The approaches that were chosen for the various problems to be discussed in subsequent sections represent tentative solutions which, at the moment, seem to be the best available, and are certainly not grossly incorrect. The particular methods will be indicated in the text.

## Results

The first glance at Figure 1 reveals a puzzling diversity of headings. Differences according to loft membership seem to be prevalent. I shall, therefore, first focus on loft-specific differences.

### 1. *Vanishing data*

In 22 out of the grand total of 111 releases, the birds were distributed at random (at $p > 0.05$). The highest proportion of releases with random vanishing patterns was scored by the north loft with 7 out of 20 or 35% of the releases, the lowest proportion for the central loft with 1 out of 21 or 4.8% of the releases. The other lofts scored 26% (east), 17% (south), and 17% (west) out of 23, 23 and 24 releases, respectively. These rates are inhomogeneous at $p = 0.14$ but the rate of the center loft is different at $p = 0.02$ ($\chi^2$-test) from that of the north loft. The rate of random releases was smaller (at $p = 0.055$; $\chi^2$-test) for the short-distance sites, with 5 out of 47 releases, than the rate for the longer-distance sites, with 17 out of 64 releases (including Reidsville).

Eighteen times, the first two releases disagreed, six times for the east loft and 4, 3, 3, and 2 times for the south, west, north, and central loft, respectively. The third release also disagreed with any of the first two releases, one time each for the east and the center loft.

Drastically differing directional preferences characterize primarily the diagrams of the short-distance release sites. Pigeons whose home direction differed only by a few degrees or not at all headed into diverging, sometimes into opposite, directions. No consistency is to be observed between differences in distance and di-

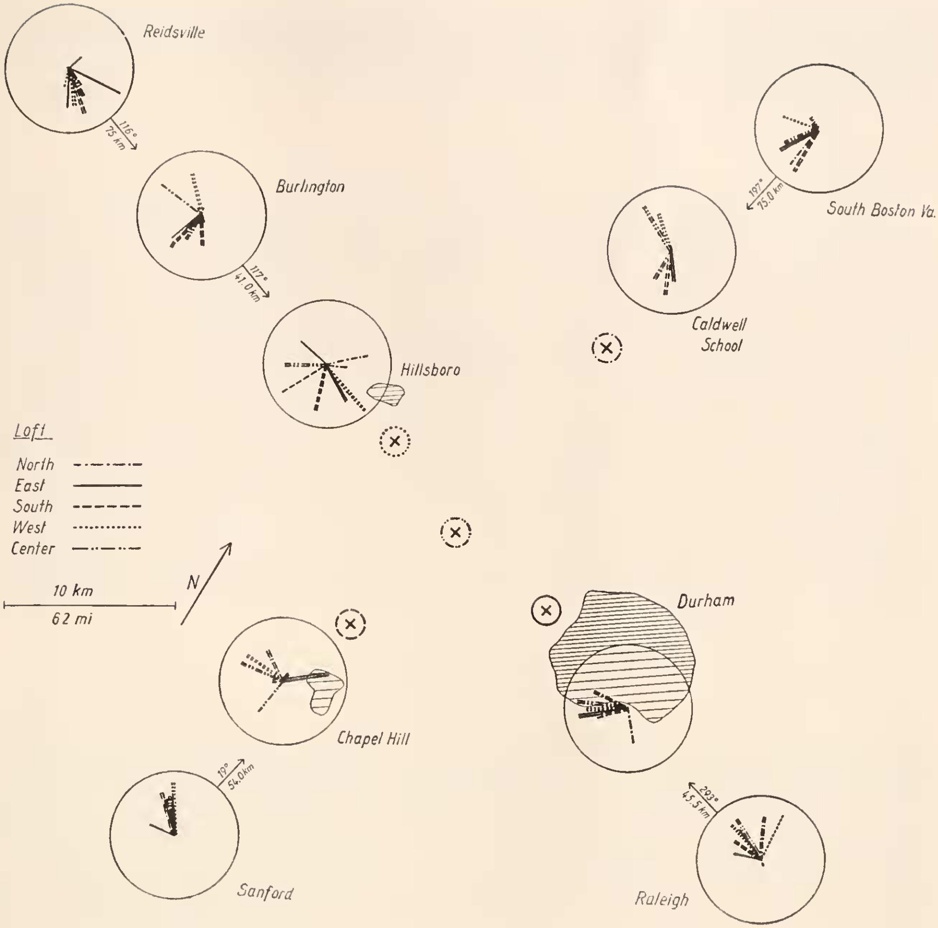


FIGURE 1. Lofts and vanishing diagrams. The location of each loft is designated by a cross encircled by its symbol (according to the key). The diagrams from the four short-distance release sites are centered according to scale, those from the five longer-distance sites are referred to the center loft with proper indications of distance and bearing at the centrifugal arrow. The vectors are given by the respective loft symbol. The radius of each diagram corresponds to 1 (unit vector). The mathematical procedure is explained in the text. The precise quantities can be read from Table I.

rection from home and the vanishing pattern of the birds from the various lofts. Even qualitative directional differences of headings do not consistently agree with corresponding differences in home direction. The reader may easily select proper examples from Figure 1 and Table I, respectively.

Although the diversity was clearly reduced at the longer-distance sites, there were still some evidently diverging directional preferences. There is also some indication that the diversity and the reduction of diversity with increasing distance varied in different directions. The least tendency for diversity seemed to be from the east, then south, and north, finally the largest from the west. This relation is supported by the finding of an overall west tendency seemingly superimposed on all headings (Fig. 3). The relation between vanishing scores and the home direction is discussed more quantitatively below.

2. *Homing success*

The rate of losses was inhomogeneous at $p = 0.07$ ($\chi^2$-test) for all lofts. However, significantly different rates ($p \leq 0.01$) between some lofts are established (north 11.8%, east 13.7%, south 9.0%, west 7.5%, center 10.9%; *cf.* Table I). Homing success is known to be much less sensitive a criterion than homing performance. There is good reason to assume that more striking differences would have been observed on the basis of individual homing speeds. Homing success from the longer-distance releases was not significantly different from that of the short-distance releases (Table I). This is easily explained since the orientational experience of the birds, as judged on the average number of releases performed, was much greater (10–20 releases) in the longer-distance releases than in the shorter-distance releases (6–12 releases). Homing performance of the Duke strain has been shown to improve steadily up to and perhaps beyond the twentieth release per bird (Schmidt-Koenig, 1963), while the tendency to scatter and homeward directedness of departures probably does not improve beyond about the eighth to tenth release (*op. cit.*).

## Discussion

1. *The distance*

The original aim of this investigation was to find out whether the initial orientation of birds facing sizably different distances, but identical home directions, or vice versa, would differ in some typical fashion. Considering the variation among the lofts and within the range tested (below 100 km.), this was clearly not so. But indications that the distance may enter into the mechanism of navigation emerge when larger dimensions than those few kilometers difference between the lofts are considered. The qualitative impression from Figure 1, that strongly diverging headings diminish with increasing distance from home, may be turned into a more quantitative consideration. In Figure 2 all vanishing scores were calculated to yield h′ the homeward component. This statistic is calculated as $h = a.\cos(\alpha\text{-}\beta)$, where a is the length of the mean vector $\alpha$ of a vanishing diagram and $\beta$ the home direction. The prime symbolizes quantities obtained upon pooling data from more than one release. Although the varying sample size and the absence of specific statistical tests render this a rather rough approach, we may note in Figure 2 some association between accuracy of headings and distance. Homeward directedness seems to improve with increasing distance insofar as violently deviating tendencies (exhibited primarily by the center- and the west-loft birds) do not occur any more. But there is no or not much improvement of accuracy within the home half of the circle ($h' > 0.0$), along with a tentative indication for an increase of random distributions for the longer distance sites (35–84 km.). One more restriction has to be made: due to the design of the experiment, the birds' orientational experience also grew with increasing distance. The lowest level of experience of any individual participant in the short-distance releases was

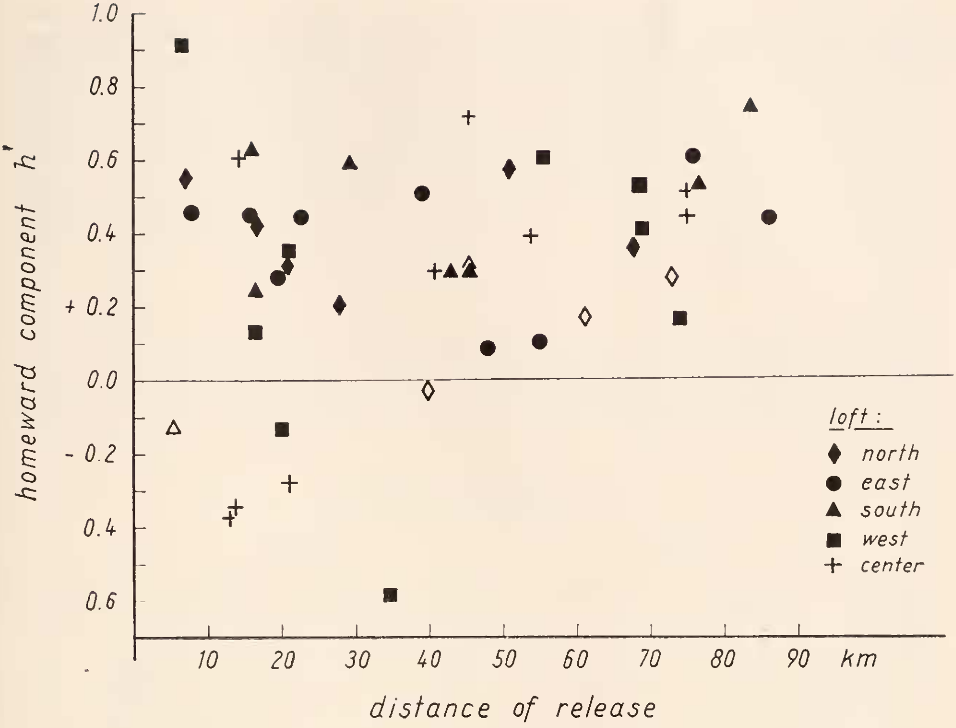


FIGURE 2. The homeward component h′ summarizing all vanishing scores per loft at each release site. Open symbols stand for distributions random at $p > 0.05$. The homeward component is positive if the mean vector of a distribution falls within the homeward half of the circle; if a mean vector falls into the other half, the homeward component becomes negative. The value $h = +1.0$ would indicate that vanishing points uniformly coincided with the home direction, $h = -1.0$ would mean all birds vanished at 180° from home. A value of $h \cong 0.0$ may indicate either that vanishing points clustered around ± 90° from the home direction or that they were distributed approximately at random.

never lower than the fourth release. In the longer-distance release sites the levels of experience were accordingly higher. Thus, the conclusion remains tentative for several reasons.

As an indication for the variance of headings, a′ was computed for the same data for which h′ was given in Figure 2. There seemed to be no reduction of scatter with increasing distance (no Figure).

## 2. *The loft*

Several authors (Pratt, 1955; Kramer, Pratt and St. Paul, 1956, 1958; Pratt and Wallraff, 1958; Graue and Pratt, 1959; Hoffmann, 1959) present or discuss indications that even consanguineous birds may differ in homing performance when settled at different geographical locations. The present study (a) extends such findings on other portions of the homing process and (b) indicates differences between lofts just a few kilometers apart from each other. The evidence of the above-mentioned publications suggested the differences were either largely due to some gross features, either topographical factors as presence or absence of mountain ranges, water bodies and the like, or to the orientational clues varying in strength or kind. Wallraff (1960a) concluded from extensive correlation analyses of variations in the performance of Wilhelmshaven colony birds that these variations, at least to some extent, were due to large scale meteorological and geophysical fluctuations. He further concluded that these variables interfere directly with the clues utilized by the birds. Such an interpretation appears to be hardly applicable to the differences and variations observed in the cross-loft experiment. They were certainly not characteristics of the general area, they affected one or two, never all lofts on a given release day. Certain release sites or even general directions seemed to be more sensitive than others in reflecting differences and variations in differences. Already Kramer, Pratt and St. Paul (1956, 1958) have come across indications for differences in the performance of the east (Duke Forest) loft, the center (Baucom) loft and the Nation Ave. loft birds near

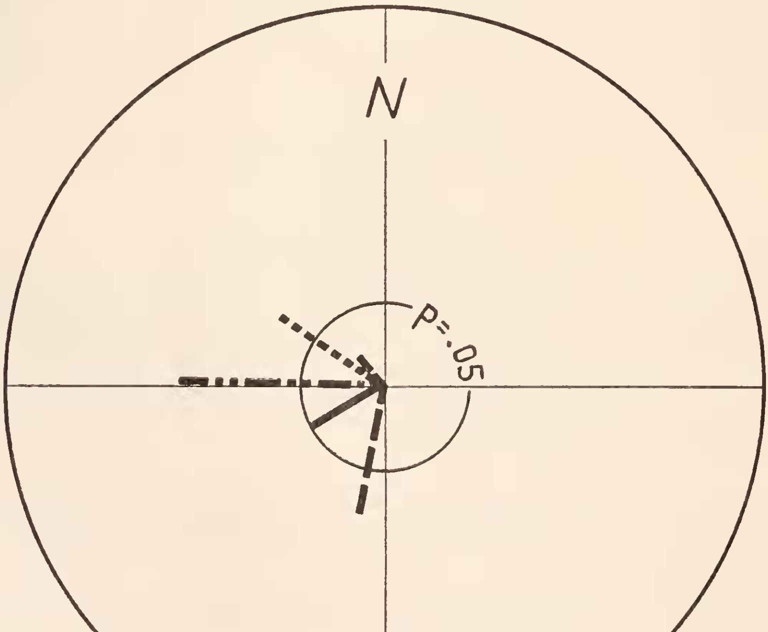


FIGURE 3. General directional tendency for each loft. To obtain a fairly symmetrical account, the first two releases of each loft at the eight main sites (exclusive of Reidsville) have been pooled. Each vector represents 230–258 vanishing scores. The radius of the circle corresponds to 1 (unit vector). The 5% level for randomness, extrapolated from Durand and Greenwood (1958, Figure 1 upper diagram) for the mean sample size (245), is indicated.

Durham. The evidence, however, was not sufficiently striking to conclude there were loft-specific factors. These authors realized that the concept of "directional differences" may have to be abandoned. Wallraff (1959a, 1959b; 1960a, 1960b) focused entirely on "local effects" for deviations of headings from the home direction and their variations. Graue and Pratt (1959) suggested not some feature at the release site but the direction of flight from a given point as contributing at least a component to the "local effect." Thus, there is a line of observations that leads to the view that the bird's goal may contribute a component to the unexplained variations in homing.

### 3. *Other aspects*

There is still a chance that a general directional tendency is superimposed on headings. For Wilhelmshaven, a north to northwest trend is well known. It is probably due to the polarized release pattern lacking flights from the north. No account is available for other loft sites in Germany. Matthews' (1955) data suggest no general directional tendency in long-distance release (up to 170 km.) in England. Graue and Pratt's data from a symmetrical release pattern on the north-south axis in California show a westerly component. In order to have a fairly, though not strictly, symmetrical total of vanishing scores for the Durham area, the data from the first two releases of the cross-loft series at the eight symmetrical release sites (exclusive of Reidsville) have been pooled for each loft. The mean vectors are given in Figure 3. A general westerly trend is evident; however, loft-specific differences again seem to prevail. The scores of the north loft are at random ($p \approx 0.1$), those of the east loft are at the edge of significance ($p = 0.05$). This may mean that the birds tended either (a) to random vanishing, which obtains for the north loft, or (b) to more homeward directed departures, which obtains for the east loft. The question of general trends possibly superimposed on headings, despite symmetrical release patterns, will be more thoroughly discussed in another paper on the basis of more detailed data from North Carolina and other areas.

## Summary

1. Five lofts which formed a symmetrical cross, with several kilometers' distance between the lofts, were established. Releases were performed with birds from all lofts along the extensions of the axes of this cross. From points close to the cross, birds from certain lofts would face identical home directions but different distances whereas birds from other lofts would face different directions but similar distances. The effect of such controlled interrelations upon initial orientation and homing success below 100 km. was studied.

2. A diversity of directional preferences, but no consistency between the variations in distance and direction from home and direction of headings, was found.

3. A loft-specific basis for the differences and changes in vanishing behavior and homing success is suggested. Its cause is unknown. Previously suggested explanations, such as large scale topographical, geophysical, and meteorological factors and variations, are hardly applicable to these observations.

4. There may be some improvement of homeward directedness of headings

with increasing distance; however, random vanishing patterns were observed up to the longest distances tested (84 km.).

5. A slight general west tendency, apparently modified by loft-specific components, was observed for the Durham area.

## LITERATURE CITED

DURAND, D., AND J. A. GREENWOOD, 1958. Modifications of the Rayleigh test for uniformity in analysis of two-dimensional orientation data. *J. Geology,* **66**: 229–238.

GRAUE, L. C., AND J. G. PRATT, 1959. Directional differences in pigeon homing in Sacramento, California and Cedar Rapids, Iowa. *Behaviour,* **7**: 201–208.

GREENWOOD, J. A., AND D. DURAND, 1955. The distribution of length and components of the sum of n random vectors. *Ann. Math. Stat.,* **26**: 233–246.

GUMBEL, E. J., J. A. GREENWOOD AND D. DURAND, 1953. The circular normal distribution: theory and tables. *J. Amer. Stat. Assoc.,* **48**: 131–152.

HOFFMANN, K., 1959. Über den Einfluss verschiedener Faktoren auf die Heimkehrleistung von Brieftauben. *J. Ornithol.,* **100**: 90–102.

KRAMER, G., 1950. Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. *Naturwiss.,* **37**: 188.

KRAMER, G., 1951. Eine neue Methode der Erforschung der Zugorientierung und die bisher damit erzielten Ergebnisse. *Proc. 10th Internat. Ornith. Congr., Uppsala,* **1950**: 269–280.

KRAMER, G., 1952. Experiments on bird orientation. *Ibis,* **94**: 265–285.

KRAMER, G., 1953a. Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *J. Ornithol.,* **94**: 201–219.

KRAMER, G., 1953b. Danebenfliegen und Überfliegen beim Heimflug von Brieftauben. *Vogelwarte,* **16**: 146–148.

KRAMER, G., J. G. PRATT AND U. v. ST. PAUL, 1956. Directional differences in pigeon homing. *Science,* **123**: 229–230.

KRAMER, G., J. G. PRATT AND U. v. ST. PAUL, 1958. Neue Untersuchungen über den Richtungseffekt. *J. Ornithol.,* **99**: 178–191.

MATTHEWS, G. V. T., 1955. Bird Navigation. Cambridge University Press.

PRATT, J. G., 1955. An investigation of homing ability in pigeons without previous homing experience. *J. Exp. Biol.,* **32**: 70–83.

PRATT, J. G., AND H. G. WALLRAFF, 1958. Zwei-Richtungsversuche mit Brieftauben: Langstreckenflüge auf der Nord-Süd-Achse in Westdeutschland. *Zeitsch. Tierpsychol.,* **15**: 332–339.

SCHMIDT-KOENIG, K., 1958. Experimentelle Einflussnahme auf die 24-Stunden-Periodik bei Brieftauben und deren Auswirkungen unter besonderer Berücksichtigung des Heimkehrvermögens. *Zeitschr. Tierpsychol.,* **15**: 301–331.

SCHMIDT-KOENIG, K., 1960. Internal clocks and homing. *Cold Spring Harbor Symposia,* **25**: 389–393.

SCHMIDT-KOENIG, K., 1961. Die Sonne als Kompass im Heim-Orientierungssystem der Brieftauben. *Zeitschr. Tierpsychol.,* **18**: 221–244.

SCHMIDT-KOENIG, K., 1963. On the role of stock, selection and experience in pigeon homing. *Animal Behaviour,* in press.

WALLRAFF, H. G., 1959a. Über den Einfluss den Erfahrung auf das Heimfindevermögen von Brieftauben. *Zeitschr. Tierpsychol.,* **16**: 424–444.

WALLRAFF, H. G., 1959b. Örtlich und zeitlich bedingte Variabilität des Heimkehrverhaltens von Brieftauben. *Zeitschr. Tierpsychol.,* **16**: 513–544.

WALLRAFF, H. G., 1960a. Über Zusammenhänge des Heimkehrverhaltens von Brieftauben mit meteorologischen und geophysikalischen Faktoren. *Zeitschr. Tierpsychol.,* **17**: 82–113.

WALLRAFF, H. G., 1960b. Does celestial navigation exist in animals? *Cold Spring Harbor Symposia,* **25**: 451–461.